

NEW ACROTRETACEAN BRACHIOPODS FROM THE PALAEOZOIC OF BRITAIN AND AUSTRIA

by L. R. M. COCKS

ABSTRACT. New acrotretacean brachiopods are described; *Caenotreta aldridgei* gen. et sp. nov. from the Llandovery of the Welsh Borderland, England, *C. celloni* sp. nov. from the Llandovery of the Carnic Alps, Austria and *Caenotreta* sp. from the late Silurian of the Carnic Alps. There are also new records from the Devonian of Germany. The possible ecology of these micromorphic conical forms is discussed.

DURING a study of Silurian conodonts (Aldridge 1972), in particular from the Welsh Borderland, Dr. R. J. Aldridge recovered some small conical shells from his acid-treated residues at several different localities and stratigraphical horizons. Subsequent collections made by him from the Silurian of the Carnic Alps, Austria, and also the Devonian of Germany, yielded similar shells which, upon examination, were found to be inarticulate brachiopods of the superfamily Acrotretacea. Comparable small shells have been described from the Ordovician, especially by Cooper (1956) from America and Biernat (1973) from eastern Europe, and from the Devonian by Ludvigsen (1974); but the only description of representatives of this group from the Silurian is in a short paper by Ireland (1961). Ireland described two new monospecific genera, *Artiotreta* and *Acrotretella* from the middle part of the Chimneyhill Formation of Oklahoma, U.S.A. The Chimneyhill is of Llandovery age.

Since Ireland's paper was written, the scanning electron microscope has become a standard tool in the study of small fossils, and enables adequate pictures of the Silurian members of the Acrotretacea to be published for the first time. In addition, in the present paper a specimen is illustrated with both valves together, an unusual occurrence at any age in this group.

SYSTEMATIC PALAEOONTOLOGY

Order ACROTRETIDA Kuhn, 1949

Superfamily ACROTRETACEA Schuchert, 1893

Discussion. Following the appearance of the Acrotretacea in the early Cambrian, the superfamily diversified until its acme in the late Cambrian and early Ordovician. Numbers became noticeably fewer by Caradoc time, and by the Silurian the Acrotretacea appears to have been represented only by the minute forms described by Ireland (1961), Ludvigsen (1974), and in this paper. In the *Treatise* (Rowell 1965, p. H 276) the upper range of the superfamily was in doubt, the only information then available being from the lower Silurian material in Ireland's paper, and also some material which Rowell himself had seen, from float ascribed to the lower Devonian Kalkburg Limestone of New York State, in which only pedicle valves were found.

Later Ludvigsen (1974) described a new scaphelasmatine, *Opsiconidion* from the lower Emsian of arctic Canada, and discussed other Devonian records, which go up to the Frasnian. Some rather fragmentary specimens, not illustrated here but probably belonging to the new genus *Caenotreta* described below, have been found by Dr. Aldridge in conodont residues from the Ballersbacher Limestone (late Emsian or early Eifelian) at its type locality near Ballersbach, and also from the Günteröder Limestone (Eifelian) at Blauer Bruch, Bad Wildungen, both localities in the Rhenish Slate Mountains in Germany.

Family ACROTRETIDAE Schuchert, 1893
Subfamily TORYNELASMATINAE Rowell, 1965
Genus CAENOTRETA gen. nov.

Type species. *Caenotreta aldridgei* sp. nov. (see below).

Age range. Silurian (Llandovery Series) to Devonian (Eifelian Series).

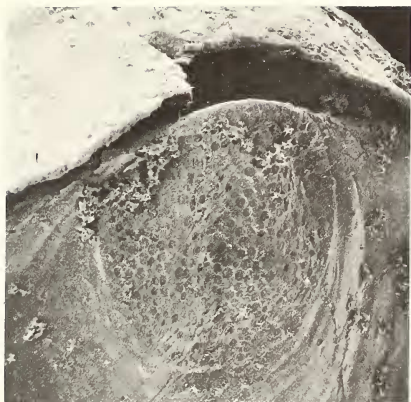
Diagnosis. Acrotretid with simple conical pedicle valve, like *Torynelasma*, but whose brachial valve has rods instead of a plate on its median septum.

Discussion. The only other genera attributed to this subfamily (Rowell 1965, p. H 279) are *Torynelasma* Cooper, 1956 and doubtfully *Acrotretella* Ireland, 1961. *Torynelasma* is now widely known from various localities and horizons in the early and Middle Ordovician; from the Pratt Ferry Formation, Alabama, U.S.A. (Cooper 1956, p. 257), the Antelope Valley Limestone, Nevada, U.S.A. (Krause and Rowell 1975), the Leningrad region, U.S.S.R. (Gorjansky 1969), Kazakhstan, U.S.S.R. (Popov 1975), Estonia and Poland (Biernat 1973) and from unpublished material from the lower Ordovician of Australia. As may be seen from the photographs of Cooper and the superb drawings of Biernat, *Torynelasma* has a very similar external shape and ornament to *Caenotreta*. The new genus also shows the distinctive protogular pattern in both brachial (Pl. 13, fig. 1) and pedicle (Pl. 14, fig. 1) valves, consisting of the honeycomb of pits described by Biernat and Williams (1970). However, *Caenotreta* differs from *Torynelasma* in possessing a pair of rods on the brachial valve median septum, instead of a plate. These rods are not unlike the early growth stages illustrated for *Myotreta* by Biernat (1973, p. 44, fig. 17), though the mature *Myotreta* possesses a

EXPLANATION OF PLATE 13

All photographs taken with the Scanning Electron Microscope.

Figs. 1-8. *Caenotreta aldridgei* gen. et sp. nov. Figs. 1, 2. BB 75901, conjoined valves, from Minsterley Formation (Llandovery, probably Fronian), Hope Brook, Minsterley, Salop. Grid Ref. SJ 360 022. Fig. 1, enlargement of brachial valve protogulum and adjoining edge of pedicle valve, $\times 500$. Fig. 2, oblique general view, $\times 100$. Figs. 3-5 from Wych Beds (Llandovery, Telychian), lane to Birches Farm, Cowleigh Park, Malvern Hills, Hereford and Worcester. Grid Ref. SO 760 468. Fig. 3, BB 75911, interior of brachial valve showing form and growth lines of the pseudointerarea, $\times 200$. Figs. 4, 5, BB 75912, holotype, oblique, and ventral views of brachial valve, $\times 100$ and $\times 50$ respectively. Figs. 6-8 from Purple Shale (Llandovery Telychian), stream bank south-west of Ticklerton, Salop. Grid Ref. SO 481 901. Fig. 6, BB 75936, oblique view of pedicle valve, $\times 60$. Fig. 7, BB 75922, lateral view of pedicle valve, $\times 50$. Fig. 8, BB 75920, exterior of smaller brachial valve, $\times 200$.



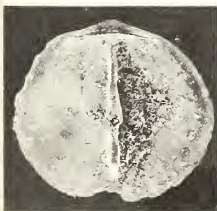
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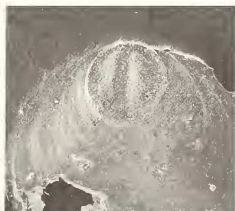
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COCKS, acrotretacean brachiopods

folded median septum (Biernat 1973, p. 84, fig. 30) quite different from *Caenotreta* or *Torynelasma*. In addition *Torynelasma* possesses a pair of muscle scars each surrounded by a prominent rim of shell material just anterior to either end of the pseudointerarea in the brachial valve interior; these rims are absent from *Caenotreta*. The only trace of muscle attachment areas on the floor of the brachial valve of *Caenotreta* is an ill-defined area of very weak flabellate scars to be seen only in one or two of the presumably more gerontic specimens (e.g. Pl. 13, fig. 4).

Acrotretella differs from *Caenotreta* in its median septum, which starts posteriorly as a pair of prongs, which merge anteriorly to form a single blade without any kind of plate, the whole structure resembling a tuning fork when viewed from above (Ireland 1961). In addition, the pedicle valve of *Acrotretella* is less sharply conical and the growth lines more prominent, but these last two features by themselves would be regarded more as specific than generic characters. Details of the pseudointerarea in *Acrotretella* are not known.

Hansotreta also has a tall conical pedicle valve which externally resembles *Caenotreta* and *Torynelasma*, but *Hansotreta* has a prominent apical process, leading to its placement in the Acrotretinae (Krause and Rowell 1975).

Caenotreta aldridgei sp. nov.

Plate 13, figs. 1-7; Plate 14, figs. 1-4

Description

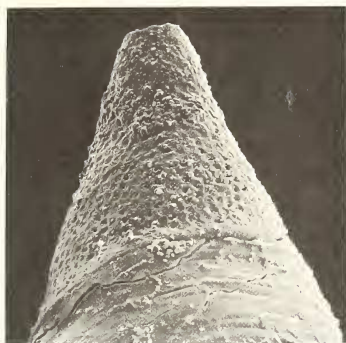
Pedicle valve. Acutely conical in shape, with posterior part of cone more rectilinear in profile than the more sloping anterior part. The pseudointerarea is indicated only by a slight asymmetry in cross-section—there are no well-defined edges to the pseudointerarea and no sign of any intertrough or interridge. Ornament absent from main part of shell, apart from fine growth lines which continue evenly round the whole anti-apical margin in mature specimens. Prominent protegulum with honeycomb of pits (Pl. 14, fig. 1), some overlapping in the same way as *Opsiconidion* (Ludvigsen 1974, fig. 4); open foramen at very apex of valve (Pl. 14, fig. 2); further enlargements of the foramen show the protegular pits of the protegular exterior continue over the edge of the foramen into valve interior; pedicle tube absent. Valve interior smooth, without visible structures of any kind (Pl. 14, fig. 4).

Brachial valve. Subcircular in outline, flat to very slightly convex, apart from a slight suggestion of a very shallow, even median sulcus (Pl. 13, fig. 2). Exterior smooth, apart from fine growth lines. Protegular area with similar ornament to pedicle valve, consisting of pits in a honeycomb arrangement (Pl. 13, fig. 1).

EXPLANATION OF PLATE 14

All photographs taken with the Scanning Electron Microscope.

- Figs. 1-4. *Caenotreta aldridgei* gen. et sp. nov. Figs. 1, 3, 4, from Purple Shale (Llandovery, Telychian), streambank south-west of Ticklerton, Salop. Grid Ref. SO 481 901. Fig. 1, BB 75925, apex of pedicle valve, showing protegulum, $\times 500$ approx. Fig. 3, BB 75918, oblique view of brachial valve, $\times 150$. Fig. 4, BB 75923, oblique view looking up into the interior of a pedicle valve, $\times 100$. Fig. 2, BB 75913, oblique view of the apex of a pedicle valve, showing the pedicle opening, $\times 500$, from Venusbank Formation (Llandovery, Idwian), Hope Quarry, near Minsterley, Salop. Grid Ref. SJ 355 021.
- Fig. 5. *Caenotreta* sp., BB 75941, lateral, but slightly oblique, view of a pedicle valve, $\times 75$, from Horizon 18 (*ploeckensis* Zone, Ludlow), Cellon section, Carnic Alps, Austria.
- Figs. 6-8. *Caenotreta celloni* gen. et sp. nov. Figs. 6-8, BB 75942, holotype, a brachial valve, Fig. 6, ventral view, $\times 50$. Fig. 7, oblique view from anterior, showing shape of septum and its rods, $\times 75$. Fig. 8, lateral oblique view, $\times 60$, from Horizon 10J (*celloni* Zone, Llandovery, Telychian), Cellon section, Carnic Alps, Austria.



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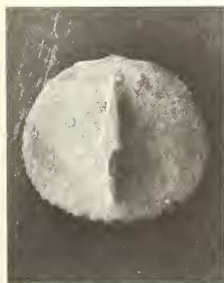
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Interior with prominent anacline pseudointerarea (Pl. 13, fig. 3), with entire growth lines and no median structures apart from a broad shallow groove. No trace of muscle scars, apart from a very slightly flabellate area, with no well-defined boundaries, anterior to the pseudointerarea in just one or two specimens (e.g. the holotype). Prominent median septum arising from valve floor just anterior to pseudointerarea, and incorporating two rods projecting antero-ventrally from the floor of the valve; an upper rod running the whole length of the top of the septum, in the position corresponding to the plate of *Torynelasma*; the lower rod diverging from the upper rod at about one-third valve length and continuing anteriorly beneath the upper rod in the septum. Both rods project further ventro-anteriorly than the septum, and end in rounded knobs (Pl. 13, fig. 4). The edge of the valve is angled round the entire margin anterior to the pseudointerarea, so as to fit snugly into the pedicle valve when the valves were together (Pl. 13, fig. 2).

Localities and material. Holotype BB 75912, a brachial valve (Pl. 13, figs. 4, 5), one of six brachial valves and two pedicle valves (including BB 75907 to BB 75912), from Wych Beds (Llandovery, Telychian), lane leading to Birches Farm, Cowleigh Park, Malvern Hills, Hereford and Worcester. Grid Reference SO 760 468. Locality C.P. 1 of Aldridge (1972). Twenty-three pedicle valves and fourteen brachial valves (including BB 75914 to BB 75940) from very top of Purple Shale (Llandovery, Telychian), stream bank south-west of Ticklerton, Salop. Grid Ref. SO 481 901. Localities Ticklerton 1 and 3 of Aldridge (1972), age later modified by Aldridge 1975, p. 612. Conjoined valves, three further pedicle valves and one further brachial valve (including BB 75901 to BB 75906) from Minsterley Formation (Llandovery, probably Fronian), bank of Hope Brook, Minsterley, Salop. Grid Ref. SJ 360 022. Locality H.V. 4 of Aldridge (1972). Probably referred to the species is a single pedicle valve (BB 75913) from Venusbank Formation (Idwian), Hope Quarry, south of Minsterley, Salop. Grid Ref. SJ 355 021. Locality H.Q. 3 of Aldridge (1972). Thus the confirmed range of the species is in the Fronian and Telychian Stages of the Llandovery Series, and probably extends from the underlying Idwian Stage.

Dimensions. Like the conodonts with which they are associated, measurement of these shells with a conventional microscope and graticules is difficult, and the range of accuracy has been only an estimated 10%. However, measurement of topotype specimens are as follows: BB 75912, holotype, a brachial valve, length 0.8 mm, width 0.9 mm; BB 75908, a pedicle valve, height 1.0 mm, width 0.8 mm; BB 75910, a brachial valve, height of median septum and rods 0.3 mm. The whole series of populations studied have comparable dimensions.

Caenotreta celloni sp. nov.

Plate 14, figs. 6-8

Description

Pedicle valve. There are no discernible differences between the pedicle valves of *C. celloni* and *C. aldridgei* (for description see above).

Brachial valve. Although the valve outline is very similar to *C. aldridgei*, and may still be termed subcircular, the outline of *C. celloni* is slightly more quadrangular, with the change in angle between lateral margins and pseudointerarea more marked than in *C. aldridgei*. Radial ornament absent; growth lines slightly coarser than in *C. aldridgei*, but protogulum of similar size and ornament. Internally the pseudointerarea is comparable with *C. aldridgei*, but the septal structure is different. In *C. celloni* the median septum rises from the valve floor just anterior to the pseudointerarea, but there is a pair of upper rods on the top of the septum (Pl. 14, fig. 7), as opposed to the single rod of *C. aldridgei*. Although this pair of rods coalesces, there is a clear median furrow between the rods, which precludes confusion with the entire plate of *Torynelasma*. There is also a lower rod, in a similar style and position to that of *C. aldridgei*. There is no trace of any muscle scars on the valve floor.

Localities and material. Holotype BB 75942, a brachial valve (Pl. 14, figs. 6-8), one of nine brachial valves and five pedicle valves (including BB 75942 to BB 75946), from Horizon 10J of Walliser (1964) (*celloni* Zone, Llandovery, Telychian), Cellaon section, Carnic Alps, Austria. Eleven brachial valves and six pedicle valves (including BB 75947 to BB 75951) from Horizon 11D of Walliser (1964) (lower part of *amorphognathoides* Zone, Llandovery, Telychian), Cellaon section, Carnic Alps, Austria.

Discussion. *Caenotreta aldridgei* and *C. celloni* are contemporary species of the late Llandovery. The chief substantial difference between the two species is in the single rod at the top of the median septum in *C. aldridgei* as opposed to the fused pair of rods seen in *C. celloni*, and this difference was observed in all of the brachial valves of the populations concerned.

Caenotreta sp.

Plate 14, fig. 5

Localities and material. From above Horizons 10J and 11D, which yielded *C. celloni*. Dr. Aldridge has collected material of *Caenotreta* from the following horizons in the Cellon section of the Carnic Alps, Austria. The terminology of the horizons and their conodont zones is from Walliser (1964), and their correlation from Aldridge (1975). Horizons 12 and 12A, upper part of *amorphognathoides* Zone (Wenlock, Sheinwoodian); Horizon 14D, upper *sagitta* Zone (Wenlock, Homeric); Horizon 16, upper *crassa* Zone (Ludlow, Eltonian); Horizons 16A, 17, 18 (including BB 75941, Pl. 14, fig. 5), *ploeckensis* Zone (Ludlow, Eltonian or slightly later); Horizon 27, *latialatus* Zone (Ludlow); Horizon 31A, *crispus* Zone (Ludlow); Horizon 39, *eosteinhornensis* Zone, just below the base of the *Megaera*-Schichten (late Ludlow or early Pridoli).

Discussion. Although there are not enough specimens from any one of these horizons for it to be safe to found a new species, the material listed above is sufficiently diagnostic both to extend the range of the new genus without doubt into the late Silurian of the Carnic Alps, and also to suggest that there exists in this later period a third and different species of *Caenotreta*, presumably descended from *C. aldridgei* or *C. celloni*. This species of Wenlock and Ludlow age has a pedicle valve similar to that of the two described species, but the diagnostic rods on the brachial valve median septum are relatively smaller, reduced in some cases to a mere swelling at the top of the septum. In some specimens the rods even appear to be absent, but this may be due to mechanical abrasion. However, in the youngest representatives of *Caenotreta*, from the Günteröder Limestone (Eifelian) of Blauer Bruch, Bad Wildungen, Germany, a distinct upper rod is still present, although the lower rod is absent in both of the only well-preserved brachial valves from the locality.

ECOLOGY

There are few known brachiopods whose adult form is as small as that of *Caenotreta*. At an adult size of around 1 mm, a single sand grain would pose a serious threat in even a medium-strength current. Modern bivalves of comparable size are known which live in a variety of depths (Moore 1977) but these are all infaunal or semi-infaunal and thus their ecology is not directly comparable with the epifaunal acrotretaceans. In view of the shape of *Caenotreta* (Pl. 13, fig. 2), the animal must have lived with the apex of its pedicle valve down if it lived on the substrate. How deeply an adult would have settled into the substrate is unknown, but probably at least half of the length of the pedicle valve would need to be buried to afford reasonable vertical stability to the shell as a whole. However, the water intake area between the two valves had to be kept as high off the sea floor as possible. The matrices in which *Caenotreta* has been found vary in size from mud (including lime-mud) to silt. The pedicle foramen remained open, and thus one may presume a pedicle functional throughout life, but the relatively small size of the opening suggests that the pedicle may have been used as a stabilizing device.

rather than as a permanent attachment mechanism. Such a minute shell living on the sea floor would have been very threatened by even weak sedimentation. *Caenotreta* may have thrived in areas kept relatively clean by weak currents, or it may have been capable of using its small pedicle in a more subtle way so as to be able to push itself upward if the sediment rain was too great, in a manner similar to that described on a larger scale for some modern terebratulides by Richardson and Watson (1975). Rowell and Krause (1973) have suggested that some other acrotretaceans may have lived as epifauna, attached either to floating plankton or to fixed algae, and hanging downwards from them. Attractive though this theory is, it seems unlikely that *Caenotreta* lived in this attitude, since the pedicle opening is so small.

Acknowledgements. I am most grateful to Dr. R. J. Aldridge for passing these specimens on to me, to Dr. M. G. Bassett and Dr. C. H. C. Brunton for reading the manuscript, and to P. C. Ensom for technical assistance.

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Typescript received 17 February 1978

Revised typescript received 21 March 1978